



Research Note

Perceptual Learning in Vernier Acuity: What is Learned?

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It has been suggested that the improvement of vernier acuity in the course of practice reflects “fine tuning” of the visual mechanisms underlying vernier acuity. Masking studies suggest that an important source of information by which the visual system may accomplish fine vernier acuity is the activity in orientation tuned channels. Therefore, we investigated whether improvement in vernier acuity after training was accompanied by systematic changes in the orientation tuning characteristics of vernier acuity (as revealed by simultaneous spatial noise masking). The results show large interindividual variation in learning vernier acuity. However, they reveal a close correspondence between the improvement in vernier acuity and the narrowing of the orientation tuning function. Thus, the results provide some support for the notion of narrowing of the orientation characteristics of vernier acuity in the course of learning.

Perceptual learning Vernier acuity Orientation tuning Spatial masking

INTRODUCTION

Practice improves performance in a wide variety of visual tasks, i.e. the ability to discriminate between visual stimuli is better after training. For instance, training has a significant effect on the perception of depth in random-dot stereograms (Ramachandran & Braddick, 1973), the discrimination of compound gratings (Fiorentini & Berardi, 1980, 1981), the discrimination of the direction of motion (Ball & Sekuler, 1982), stereoacuity (Fendick & Westheimer, 1983; Kumar & Glaser, 1993), line orientation judgments (Vogels & Orban, 1985), texture discrimination (Karni & Sagi, 1991, 1993) and the discrimination of spatial detail, such as vernier acuity (Fahle & Edelman, 1993; Levi & Klein, 1985; McKee & Westheimer, 1978; Poggio, Fahle & Edelman, 1992; see however, Bennett & Westheimer, 1991).

These perceptual learning effects seem to be specific for a visual field location (Fiorentini & Berardi, 1981; Karni & Sagi, 1991) and for some fundamental stimulus dimensions, such as orientation, spatial frequency and the direction of motion (Ball & Sekuler, 1982; Fahle & Edelman, 1993; Fiorentini & Berardi, 1980, 1981; Poggio *et al.*, 1992). For instance, if the observer practices vernier acuity for vertical lines, there is no transfer of learning to vernier acuity measured for horizontal lines (Fahle & Edelman, 1993; Poggio *et al.*, 1992).

While many factors may contribute to general learning effects, one suggestion for *specific* learning is that performance improvement due to training might represent a kind of “fine tuning” in the mechanisms underlying these visual tasks (e.g. McKee & Westheimer, 1978). As Fiorentini and Berardi (1980, 1981) have pointed out, the specificity of learning for orientation, spatial frequency and a visual field location may suggest that the possible “fine tuning” is likely to take place at the early stages of visual processing. Of course, the results of perceptual learning studies do not exclude the possibility that some higher-level processes may also contribute to the practice effects (e.g. learning to attend to critical stimulus cues).

In the present study, perceptual learning (threshold decrease due to practice) was investigated in a vernier acuity task (i.e. observers practiced the detection of an offset between two abutting line segments). We chose the vernier task because it is a “hyperacuity” task which is thought to be mediated by fairly low-level, probably cortical, visual mechanisms (Wilson, 1986; Klein & Levi, 1985). Several lines of evidence suggest that the activity in the orientation tuned channels (Campbell & Kulikowski, 1966; Phillips & Wilson, 1984) represents an important source of information by which the visual system may accomplish vernier acuity (e.g. Findlay, 1973; Sullivan, Oatley & Sutherland, 1972; Watt, Morgan & Ward, 1983; Waugh, Levi & Carney, 1993; Wilson, 1986). Therefore, the question we address in this Research Note is whether improvement in vernier acuity due to training is accompanied by a change in the orientation tuning characteristics of vernier acuity.

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In order to answer this question, the orientation tuning characteristics of vernier acuity were determined in each phase of practice using the paradigm of simultaneous spatial masking (Campbell & Kulikowski, 1966; Findlay, 1973; Phillips & Wilson, 1984; Waugh *et al.*, 1993), i.e. vernier thresholds were measured as a function of the orientation of a spatial noise mask. Using the masking paradigm with similar stimuli and psychophysical task to those of the present study, Waugh *et al.* (1993) have previously shown highly specific orientation tuning. In their highly practiced observers, vernier thresholds were most elevated when the orientation of the mask was at an angle (≈ 10 deg) away from the orientation of the vernier lines.

Figure 1 illustrates schematically three (of many possible) ways in which the orientation tuning of vernier acuity could be influenced by training. For example, Fig. 1(A) illustrates a general improvement for all the mask orientations after practice (a uniform translation of the tuning curve downward). This might occur if the learning was not mediated by orientation tuned mechanisms. Similarly, an attentional explanation (such as learning to ignore the mask) would be expected to result in a uniform improvement in performance. Figure 1(B) illustrates a shift in the peak of the

orientation tuning function after training. This sort of change might reflect a change in strategy, where the observer learned to use a more sensitive oriented channel. Figure 1(C) illustrates the more interesting case, where learning results in a selective improvement (lowering of threshold) at orientations away from the peak, i.e. a narrowing of the tuning function.

To anticipate the results, interindividual differences in the degree of learning turned out to be large; but our results show that narrowing of the orientation tuning accompanies and is more or less proportional to the improvement in (unmasked) vernier acuity.

METHODS

Stimuli

The stimuli and psychophysical methods have been described in detail by Waugh *et al.* (1993). Thus, only the main features are described here. The horizontal vernier lines and the spatial noise patterns of varying orientation were generated using a Neuroscientific VENUS stimulus generator with a frame rate of 270 Hz. The stimuli and masks were presented on a Tektronix 608 oscilloscope screen with a P31 yellow-green phosphor. The luminance of the blank oscilloscope screen was 100 cd/m². The stimuli were viewed through a circular aperture (1.15 deg dia), which was surrounded by an area of lower luminance (10 cd/m²).

The observer viewed the stimuli binocularly from a distance of 4 m with normal overhead (fluorescent) illumination. No chinrest or headrest were used because we wanted the observer to remain comfortable so that he could concentrate on the task. Vernier acuity was measured for two short abutting horizontal dark line segments, the contrast of which was 40% in all experimental conditions. The length and width of each line segment (both in the presence and absence of the spatial mask) were 10 and 0.92 min arc respectively. In the threshold measurements, the two line segments were aligned or there was a vertical offset between the lines. The use of short lines was the most important difference from the experiments described by Waugh *et al.* (1993). In pilot studies we determined that short lines minimized the perceptual tilt effects evident with longer lines, while providing sharp orientation tuning.

The spatial noise mask of two octave bandwidth (5.3–21.4 c/deg) consisted of an integer number (22) of sinusoidal wave components. Because the sinusoidal components of the mask pattern were added together in random phase, the luminance profile of the mask varied randomly from trial to trial. The contrast of the spatial mask (or the peak to peak variation of the luminance profile of the noise) was 30%. Seven orientations of the mask were used: 5, 10, 15, 20, 30, 45, and 90 deg.

The simultaneous presentation of the mask pattern and the vernier line segments was accomplished by interleaving the mask and the vernier lines frame by frame (every 3.7 msec). In those vernier acuity measurements in which the line segments were unmasked, the lines were interleaved with a frame having the

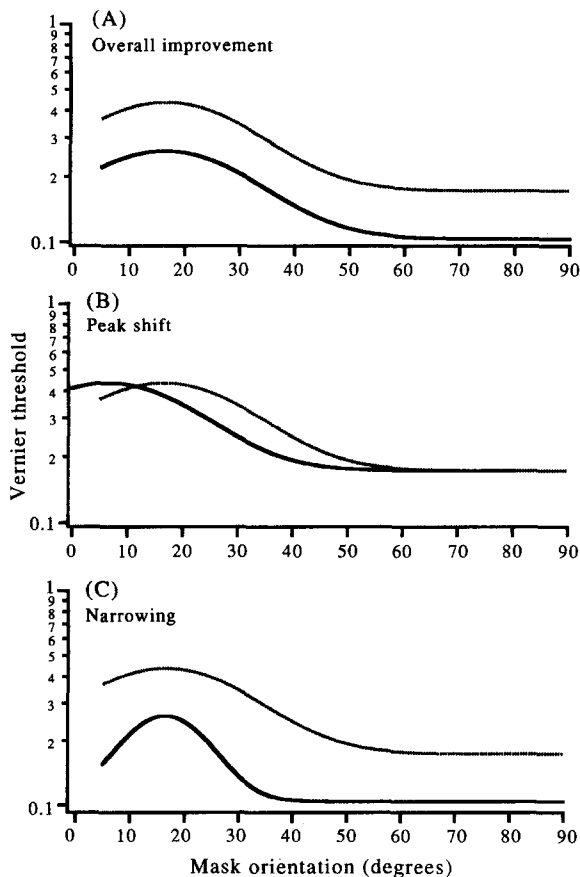


FIGURE 1. Schematic illustration how the orientation characteristics of vernier acuity might change after training: (A) overall improvement, (B) peak shift, and (C) narrowing of the orientation tuning. The curves illustrate schematically how vernier thresholds (in min arc) might depend upon the orientation of a noise mask relative to the orientation of the vernier lines.

mean luminance. The stimulus duration was 2 sec in all experimental conditions.

Psychophysical task

To obtain a criterion-free estimate of performance, a self-paced method of constant stimuli was used in the estimation of vernier thresholds. On each trial, the left line segment could randomly be in one of four equally spaced (near threshold) positions: the two lines were exactly aligned or the left line was 1, 2 or 3 steps above the right line. Three step sizes (0.18, 0.31, or 0.61 min arc) were used in the experiments, the step size depending on the observer's performance. The observer rated the offset size (0, 1, 2, or 3) and gave his response by pressing one of the four keys in the response box. If the observer was not sure about the response, he was required to guess. Auditory feedback indicating the actual position of the left line was given immediately after each response.

A threshold estimate was calculated from a block of 100 trials using the ROCFLEX signal detection analysis program (Klein & Levi, 1985). Each threshold estimate represents the smallest offset size (in min arc) which the observer could discriminate (at $d' = 1$) from no offset.

Training

One training session contained eight blocks of 100 trials (800 trials), and the entire training consisted of 10 sessions (8000 trials per observer) on separate days. Each session began with a threshold measurement for unmasked vernier acuity (100 trials), after which vernier acuity in the presence of the spatial mask was determined for the seven different orientations of the mask pattern (5, 10, 15, 20, 30, 45 and 90 deg; 100 trials per each orientation). The presentation order of mask orientation was systematically varied (from 5 to 90 deg or vice versa) and counterbalanced across the training sessions.

In addition to these basic eight blocks per session, there were some extra blocks of 100 trials in order to check the appropriate offset size. The number of these extra blocks was, however, very low (1–2 blocks for each observer in the whole experiment). Hence, their importance for the whole experiment was negligible.

In the first session, the observer was instructed about the vernier task when the unmasked vernier offset was clearly visible (from a viewing distance of 1–2 m). Before the actual training and data collection, the observer had a few preliminary trials in the first session for practicing the offset rating. One training session lasted about 2 hr. The observer was informed about his progress as the training proceeded. The length of the whole training period of 10 sessions (2–4 weeks) depended on the observer's schedule.

Observers

Four paid male observers (JC, ML, NP, and TS) from the College of Optometry participated in the vernier acuity training. No pretesting was employed for selecting

the observers. The observers had normal or corrected-to-normal vision. None of them (except NP) had any prior experience in vernier acuity measurements. NP had been an observer in a vernier acuity study approximately 2 yr previously in which vernier acuity in the peripheral visual field (but not in the central vision) was trained. Despite the previous practice, NP's improvement in the unmasked vernier acuity was the largest of the four observers (see Results).

Three training sessions had to be discontinued; two with observer NP and one with observer JC. In both cases the thresholds were sharply increased when compared to the thresholds in the previous sessions. The reason for the increase of thresholds might be fatigue (JC) and allergic symptoms (NP). Both observers had extra sessions and blocks in order to reach the total number of 10 training blocks for unmasked vernier acuity and for each mask orientation.

RESULTS AND DISCUSSION

Unmasked vernier thresholds

Figure 2 shows unmasked vernier thresholds as a function of the order of practice blocks, plotted separately for each observer. A simple regression line was fitted to each observer's data in order to test the statistical significance of improvement. The slopes of the regression lines and the confidence level with which they differ from zero are also shown in Fig. 2.

The interindividual differences were striking: NP's vernier thresholds decreased by a factor 6, whereas there was no significant change in JC's thresholds in the course of the training. The spectacular practice effect in NP's performance may be partly explained by non-perceptual factors. For instance, he might have been still learning the task of offset rating and the use of feedback in the first session. However, even if the first

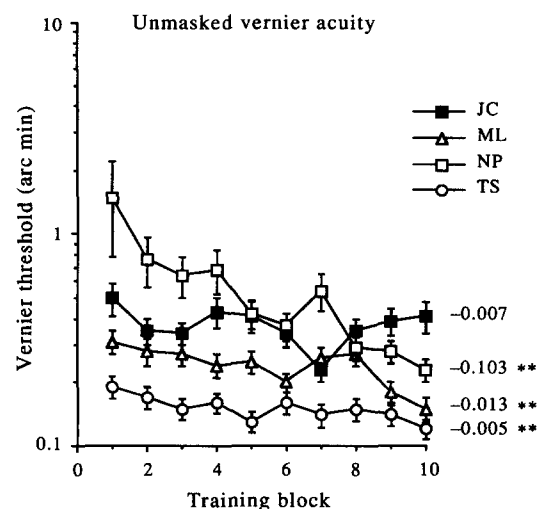


FIGURE 2. Unmasked vernier thresholds (min arc) as a function of the order of the training blocks (1–10) for each observer (JC, ML, NP, and TS). Vertical bars show \pm SE of each threshold estimate. The slope of the line fit is indicated at the end of each curve. When the slope differs significantly from zero, it is indicated by $**P < 0.01$.

session is not taken into account, his thresholds still decreased by a factor of 3. ML and TS had smaller but statistically significant training effect in their vernier acuity: ML's thresholds decreased approx. 50% and TS's thresholds 30% (from the first to last training block).

The present results showing large individual variation in the effect of training on vernier acuity are in agreement with previous learning studies (Fahle & Edelman, 1993; McKee & Westheimer, 1978). For instance, McKee and Westheimer (1978) reported that after 2000–2500 practice trials, the range of the individual decrease in vernier thresholds was from 2% to 70%. The individual variation in McKee and Westheimer's (1978) study might have been even larger if they had not employed a pretest for selecting the observers. In their pretest, those individuals were screened to serve as observers who had the best initial vernier thresholds.

Masked vernier thresholds

The orientation tuning characteristics of vernier acuity were obtained in each phase of practice using the spatial masking technique described above: the vernier stimulus lines were masked by a simultaneous spatial noise pattern of 5, 10, 15, 20, 30, 45, and 90 deg in orientation.

The masked vernier thresholds as a function of the order of the training blocks (separately for each observer) are depicted in Fig. 3. For the sake of clarity, the data for only three mask orientations (5, 20 and 90 deg) are shown. In an attempt to analyze quantitatively the changes in the orientation tuning of vernier acuity due to training, we first fitted a simple regression line to the masked thresholds, separately for each of the seven mask orientations. The preliminary analysis using linear fits suggested that the thresholds decreased relatively more at those mask orientations which were away from the orientation producing the largest threshold elevation (Table 1).

However, we felt that this analysis was not very satisfactory, because in many cases, the improvement in the masked thresholds was quite non-linear, and we were unable to find a simple, general non-linear function which could have made possible comparisons between the threshold changes at various mask orientations (although we tried several non-linear functions, including exponentials and polynomials).

Since our main interest was to assess the effect of training on the shape of the orientation tuning function, we compared the tuning curves of vernier acuity (i.e. the masked vernier thresholds as a function of the mask orientation) obtained initially with those obtained at the end of the training. Specifically, we used the weighted average (Klein, 1992) of the first two blocks (for each mask orientation) as the baseline, and compared this to the weighted average of the last two blocks.

Vernier thresholds before (open symbols) and after (solid symbols) practice are shown in Fig. 4, and the

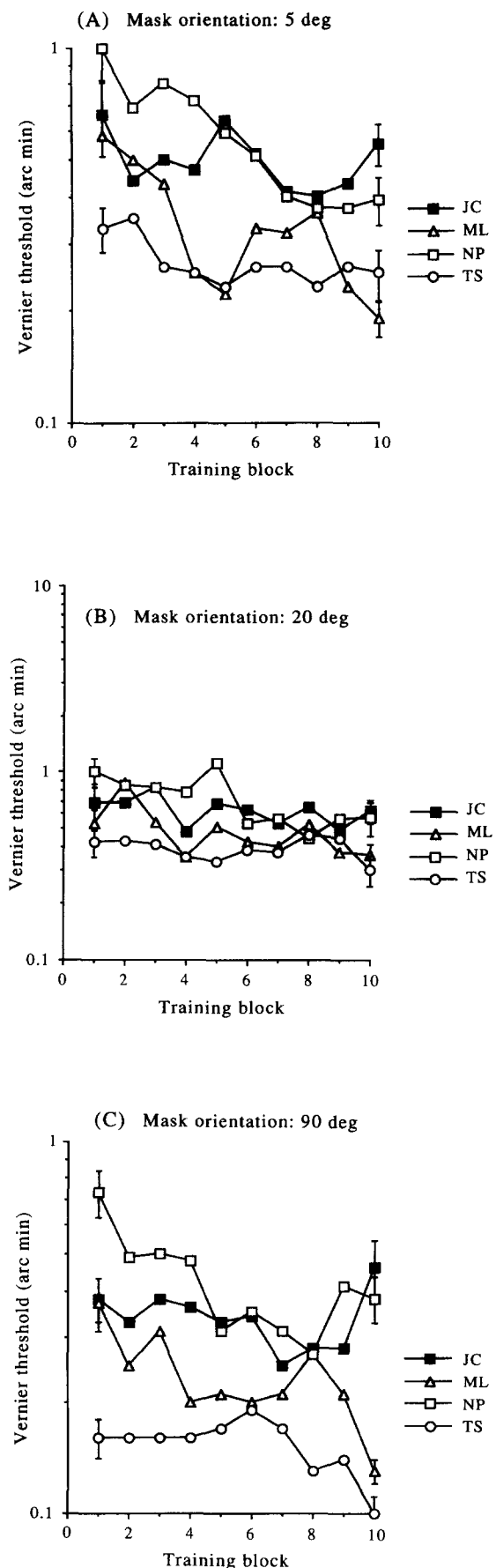


FIGURE 3. Masked vernier thresholds (min arc) plotted against the order of the training blocks (1–10) for the mask orientations of 5, 20, and 90 deg. Vertical line segments show ± 1 SE of each threshold estimate.

TABLE 1. The slopes of regression lines (min arc/practice block) fitted separately to each mask orientation

Observer	Mask orientation (deg)						
	5	10	15	20	30	45	90
JC	-0.011	0.007	-0.028	-0.017	-0.009	-0.019*	-0.003
ML	-0.033‡	-0.016*	-0.006	-0.031*	-0.034§	-0.017*	-0.016†
NP	-0.066§	-0.108‡	-0.080†	-0.055†	-0.091§	-0.048†	-0.032†
TS	-0.009†	-0.005	0.012	-0.004	-0.013*	-0.008‡	-0.005*

If the slope differs significantly from zero, it is indicated by * $P < 0.10$; † $P < 0.05$; ‡ $P < 0.01$; § $P < 0.001$.

curves used to describe and quantify the data are Gaussian functions, the form of which is:

masked threshold = base +

$$\text{elev} * \exp(-((\text{orient} - \text{orient}_p)/\text{SD})^2)$$

where base is the baseline threshold value, elev is the elevation from the baseline to the peak threshold value, orient_p is the orientation at which the peak is reached, and SD is the standard deviation of the Gaussian

function. We used Igor™ to fit the data, and estimate the best fitting parameters (which are listed in Table 2). Of particular interest is whether there was narrowing in the orientation tuning of vernier acuity after training, which would be reflected in a decrease of the SD of the Gaussian function.

The results suggest that there was indeed some narrowing in the orientation characteristics of vernier acuity, i.e. there was not just general improvement in the masked thresholds. A paired t -test including all four

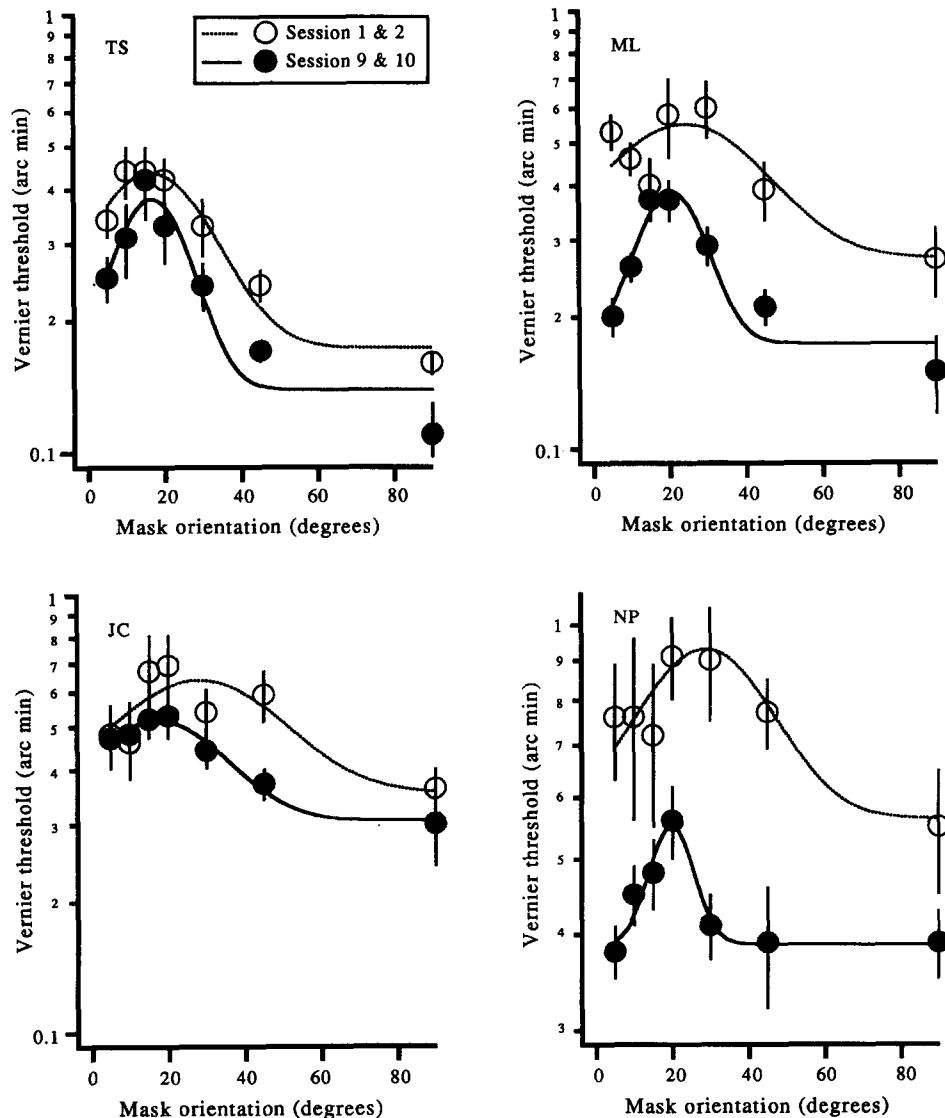


FIGURE 4. Masked vernier thresholds (min arc) plotted against mask orientation before and after practice. ○ The weighted average of the first two blocks; ● the weighted average of last two blocks of the training. Curves fitted to the data are Gaussians (see Table 2 for parameters).

TABLE 2. The standard deviation (SD) and peak parameter (orient_p) of the best fitting Gaussian functions of the orientation tuning before and after training

Observer		Standard deviation (SD)	Peak (orient_p)
JC	Before	28.4 ± 17.0	28.2 ± 6.8
	After	23.4 ± 3.8	17.2 ± 1.8
ML	Before	27.4 ± 15.1	24.2 ± 6.3
	After	11.9 ± 2.2	20.6 ± 1.3
NP	Before	26.7 ± 8.7	28.3 ± 3.7
	After	7.87 ± 1.5	19.8 ± 1.1
TS	Before	20.8 ± 4.0	16.5 ± 1.8
	After	13.4 ± 3.0	16.6 ± 1.7

observers showed that orientation tuning functions (the SDs of Gaussian fits) were significantly narrower after training than initially [$t(3) = 3.57$, $P < 0.05$]. However, this overall analysis does not reveal the large individual differences. For example, inspection of Table 2 reveals that JC, who showed no significant improvement in his unmasked thresholds, also showed little change in the orientation tuning. On the other hand, observers ML, NP and TS all had a significant decrease in standard deviation, indicating a narrowing in their orientation tuning.

In order to analyse the temporal course of the narrowing of the orientation tuning, the SDs of the Gaussian fits were plotted as a function of practice (Fig. 5). The individual differences were large, but each observer's temporal course seems to be in agreement with his orientation tuning functions before and after practice (shown in Fig. 4). The standard deviations of the Gaussian fits in JC's thresholds were constant through the training, whereas ML and TS had a steady decrease, and NP had an abrupt narrowing in the last two training blocks.

The orientation (orient_p) at which vernier thresholds were most elevated was not significantly altered by

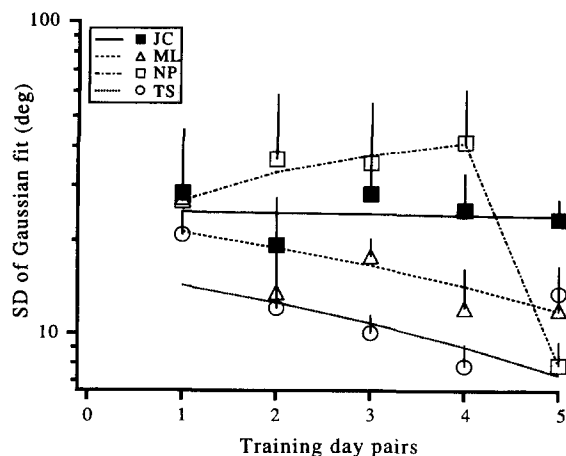


FIGURE 5. The SD (deg) of the best fitting Gaussian as a function of training. Each data point is based on an average of two consecutive training blocks. One (JC, ML and TS) or two (NP) straight lines were fitted to data to describe the change of the orientation tuning in the course of practice.

practice. The average of the peak masking orientation of the four observers was 24 deg before practice and 19 deg after practice, and a paired t -test indicated that this change was not significant [$t(3) = 2.32$, $P > 0.05$]. The peak masking orientation in the present results is larger than that reported by Waugh *et al.* (1993) who used an identical masking paradigm with similar stimuli and psychophysical task. The difference in the peak masking orientation is most likely a consequence of the difference in the length of the vernier lines. In Waugh *et al.*'s (1993) experiments, the line segments were three times longer than in this study, and Waugh and Levi (unpublished results) have shown that the peak shifts to larger orientations when vernier line length is decreased.

To summarize, because the thresholds decreased relatively more after training at those mask orientations which were away from the orientations producing the peak threshold elevation, simple explanations based on non-perceptual factors (such as gradual learning of the rating technique) may be excluded. These explanations would predict an equal improvement for all the seven mask orientations. It is also unlikely that the observers were just simply learning something specific for the task of the spatial masking (e.g. learning to ignore the mask pattern) since this might be expected to also produce a non-selective improvement for all the masked thresholds.

Relationship between masked and unmasked thresholds

There was only a slight (and non-significant) change in the standard deviation of JC's tuning curve after practice. The absence of the narrowing effect in JC's masked vernier thresholds may reflect the fact that he had no improvement in his unmasked vernier thresholds following training.

The relationship between the improvement in unmasked vernier acuity and the narrowing of the tuning curves is shown by plotting [Fig. 6(A)] the SDs of the Gaussian fits against unmasked vernier thresholds in the beginning (open symbols) and at the end of the training (solid symbols). This plot reveals an interesting parallelism between the unmasked vernier thresholds and the narrowing of the tuning curves. Note that on log-log coordinates, the slope for the three observers who "learned" is approx. 1 (1.24 ± 0.29), suggesting that the change in SD is linearly proportional to the change in vernier acuity: if the observer's unmasked thresholds improved after practice (ML, NP and TS), there was a proportional decrease in the SD of the corresponding tuning curve.

In Fig. 6(B), the relationship between the percentage of improvement in unmasked vernier acuity and the percentage of narrowing of orientation tuning is shown. This plot, like Fig. 6(A) also shows a very strong correlation between the amount of "sharpening" of the tuning curves and the benefit in unmasked vernier acuity. However, the interesting new point revealed in this plot is that our observers' learning falls along a continuum, from no improvement (JC) to rather substantial improvement ($\approx 70\%$ for NP), and the

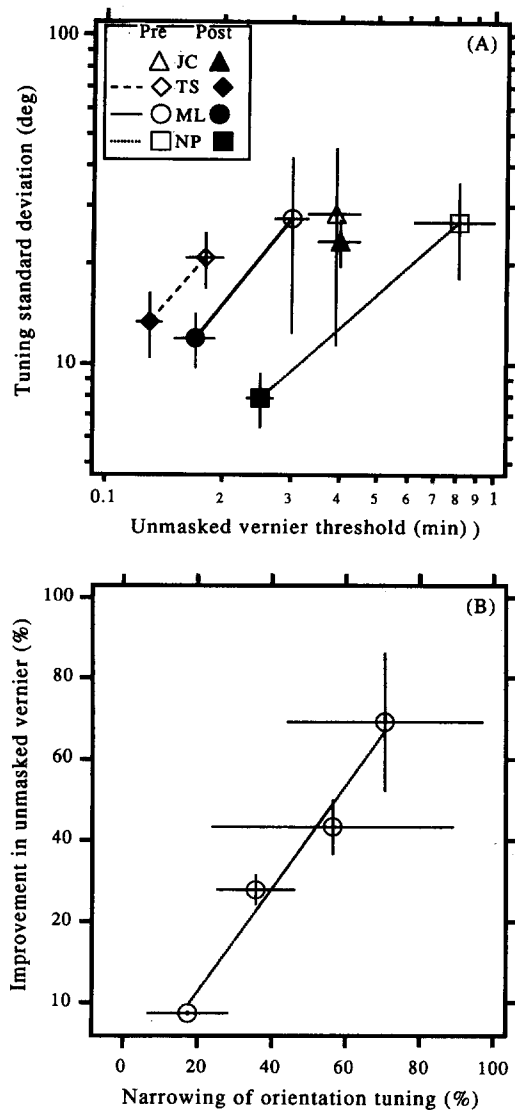


FIGURE 6. (A) The narrowing of the orientation tuning (i.e. the SD of the best fitting Gaussian) plotted against the unmasked vernier thresholds in the beginning (○) and at the end of the training (●) for each observer (JC, ML, NP, and TS). (B) Percentage of improvement in unmasked vernier thresholds plotted against the percentage of narrowing in orientation tuning. In both figures horizontal and vertical line segments show ± 1 SE.

alteration in orientation tuning appears to fall along a similar continuum.

It should be emphasized that this correlation does not necessarily imply a causal relationship, but it is consistent with the notion that improvement in vernier acuity after training might reflect "fine tuning" of the orientation sensitive mechanisms underlying vernier offset detection. The almost proportional improvement of unmasked thresholds and the narrowing of the tuning curves suggests that there might be a close link between the two.

On the other hand, it seems that the temporal course of the improvement of unmasked vernier and that of the narrowing of orientation tuning can be somewhat different: NP improved steadily in his unmasked vernier acuity, but he did not have a narrowing in the orientation tuning until in the last two training blocks (Fig. 5).

The other two observers (ML and TS) who had an improvement in their unmasked vernier thresholds had more compatible change in orientation tuning.

Off-axis looking

One possible explanation for the apparent narrowing of orientation tuning is that our observers learned to use "off-axis looking" (Blake & Holopigian, 1985), by analogy to the off-frequency listening which has been reported in audition (Leshowitz & Wightman, 1971; Patterson & Nimmo-Smith, 1980). That is, it could be speculated that the observers learned to adopt a strategy of using non-optimal orientation mechanisms to perform the task, resulting in an apparent narrowing of the tuning function. Although we cannot rule this explanation out completely, we feel that it is unlikely for two reasons: Firstly, there is no *a priori* reason that off-axis looking would result in a proportional improvement of the unmasked thresholds. Secondly, the two authors participated in a separate experiment on the effects of masking on vernier acuity with oblique lines. JS showed no effect of practice on (unmasked) vernier with oblique targets, and no change in orientation tuning after practice. DL showed an approx. 30% improvement in unmasked vernier acuity, and a commensurate narrowing of the orientation tuning. Prior to this experiment DL had completed well over 200,000 trials of masked vernier acuity using the identical paradigm but horizontal lines. Thus, it seems unlikely that the narrowing of his tuning function reflected learning the strategy of off-axis looking.

Speculations on learning mechanisms

Traditional models of early visual processing (e.g. Phillips & Wilson, 1984; Wilson, McFarlane & Phillips, 1983) assume that stimulus patterns are encoded by orientation specific spatial filters which are not adaptive in adults, i.e. the filters are "hard-wired" so their tuning properties do not change in the course of visual experience beyond the "sensitive periods" [for an interesting analysis of this issue, see Kumar and Glaser (1993)]. One possible interpretation of the present results is that these spatial filters might not be quite as fixed as has been assumed [cf. Poggio *et al.*'s (1992) model of "task-specific modules" in the early vision]. The notion of adaptive filters is in agreement with the recent neurophysiological results revealing plasticity of the visual cortex of the adult mammals—even such a "hard-wired" structure as the retinotopic map in the visual cortex can reorganize (Heinen & Skavenski, 1991; Chino, Kaas, Smith, Langston & Cheng, 1992; Gilbert & Wiesel, 1992; Kaas, Krubitzer, Chino, Langston, Polley & Blair, 1990).

There is also some neurophysiological evidence suggesting that the tuning properties of cortical receptive fields (at least at the level of V4) are dependent on "higher-level" mechanisms. For instance, single cell recordings in monkey visual cortex (Spitzer, Desimone & Moran, 1988) showed that attention makes neural responses stronger and more selective. In their study, the

orientation tuning functions of single cells in area V4 became significantly narrower when the monkey paid more attention to the stimulus line segment. Hence, there is a possibility that perceptual learning effects reflect the influence of "higher-level" mechanisms on early vision, i.e. "learning to attend" to relevant stimulus features and the "sharpening" of tuning curves due to increased attention may partly underlie perceptual learning. In this vein, it is worth noting that Waugh *et al.* (1993), suggested that the orientation tuning function for vernier acuity revealed by simultaneous masking may reflect the properties of a "second-stage" mechanism which combines information from two or more oriented filters.

An alternative suggestion* is that the particular orientation mechanism that signals the vernier offset may itself be composed of the responses of a large number of neurons. Some of these neurons may be somewhat broadly-tuned and others more narrowly-tuned for orientation. It is possible then, that the reorganization produced by learning may represent a selective weighting of the neurons that comprise the psychophysical mechanism, such that the narrowly-tuned neurons are given more weight. In this scheme, the overall tuning of the mechanism is altered by practice, but the tuning of the individual neurons that comprise the mechanism are unaltered. In this scheme, no reorganization of the receptive fields of individual neurons is required.

SUMMARY

We measured changes in both unmasked vernier acuity, and the orientation tuning characteristics of vernier acuity following extensive practice. It should be emphasized that in the present paradigm, the observers practiced both unmasked and masked vernier, so the determination of the orientation tuning characteristics of vernier acuity in each training session was a learning task *per se*. Our initial expectation was that the observers might learn to (partially) ignore the masks, resulting in a general improvement of masked vernier thresholds [Fig. 1(A)], and the observers' orientation tuning might be expected to change independently of changes in unmasked vernier acuity. Surprisingly, the present results suggest that improvement in vernier acuity is accompanied by an approximately proportional narrowing of the orientation tuning function.

REFERENCES

- Ball, K. & Sekuler, R. (1982). A specific and enduring improvement in visual motion discrimination. *Science*, 218, 697-698.
 Bennett, R. G. & Westheimer, G. (1991). The effect of training on visual alignment discrimination and grating resolution. *Perception & Psychophysics*, 49, 541-546.
 Blake, R. & Holopigian, K. (1985). Orientation selectivity in cats and humans assessed by masking. *Vision Research*, 25, 1459-1467.

- Campbell, F. W. & Kulikowski, J. J. (1966). Orientational selectivity of the human visual system. *Journal of Physiology*, 187, 437-445.
 Chino, Y. M., Kaas, J. H., Smith, E. L. III, Langston, A. L. & Cheng, H. (1992). Rapid reorganization of cortical maps in adult cats following restricted deafferentation in retina. *Vision Research*, 32, 789-796.
 Fahle, M. & Edelman, S. (1993). Long-term learning in vernier acuity: Effects of stimulus orientation, range and of feedback. *Vision Research*, 33, 397-412.
 Fendick, M. & Westheimer, G. (1983). Effects of practice and the separation of test targets on foveal and peripheral stereoacuity. *Vision Research*, 23, 145-150.
 Findlay, J. M. (1973). Feature detectors and vernier acuity. *Nature (London)*, 241, 135-137.
 Fiorentini, A. & Berardi, N. (1980). Perceptual learning specific for orientation and spatial frequency. *Nature (London)*, 287, 43-44.
 Fiorentini, A. & Berardi, N. (1981). Learning in grating waveform discrimination: Specificity for orientation and spatial frequency. *Vision Research*, 21, 1149-1158.
 Gilbert, C. D. & Wiesel, T. N. (1992). Receptive field dynamics in adult primary visual cortex. *Nature (London)*, 356, 150-152.
 Heinen, S. J. & Skavenski, A. A. (1991). Recovery of visual responses in foveal V1 neurons following bilateral foveal lesions in adult monkeys. *Experimental Brain Research*, 83, 670-674.
 Kaas, J. H., Krubitzer, L. A., Chino, Y. M., Langston, A. L., Polley, E. H. & Blair, N. (1990). Reorganization of retinotopic cortical maps in adult mammals after lesions of the retina. *Science*, 248, 229-231.
 Karni, A. & Sagi, D. (1991). Where practice makes perfect in texture discrimination: Evidence for primary visual cortex plasticity. *Proceedings of the National Academy of Science, U.S.A.*, 88, 4966-4970.
 Karni, A. & Sagi, D. (1993). The time course of learning a visual skill. *Nature (London)*, 365, 250-252.
 Klein, S. A. (1992). An Excel macro for transformed and weighted averaging. *Behavior Research Methods, Instruments & Computers*, 24, 90-96.
 Klein, S. A. & Levi, D. M. (1985). Hyperacuity thresholds of 1 sec: Theoretical predictions and empirical validation. *Journal of the Optical Society of America A*, 2, 1170-1190.
 Kumar, T. & Glaser, D. A. (1993). Initial performance, learning and observer variability for hyperacuity tasks. *Vision Research*, 33, 2287-2300.
 Leshowitz, B. & Wightman, F. L. (1971). On-frequency masking with continuous sinusoids. *Journal of the Acoustical Society of America*, 49, 1180-1190.
 Levi, D. M. & Klein, S. A. (1985). Vernier acuity, crowding and amblyopia. *Vision Research*, 25, 979-991.
 McKee, S. P. & Westheimer, G. (1978). Improvement in vernier acuity with practice. *Perception & Psychophysics*, 24, 258-262.
 Patterson, R. D. & Nimmo-Smith, I. (1980). Off-frequency listening and auditory-filter asymmetry. *Journal of the Acoustical Society of America*, 67, 229-245.
 Phillips, G. C. & Wilson, H. R. (1984). Orientation bandwidths of spatial mechanisms measured by masking. *Journal of the Optical Society of America A*, 1, 226-232.
 Poggio, T., Fahle, M. & Edelman, S. (1992). Fast perceptual learning in visual hyperacuity. *Science*, 256, 1018-1021.
 Ramachandran, V. S. & Braddick, O. (1973). Orientation specific learning in stereopsis. *Perception*, 2, 371-376.
 Spitzer, H., Desimone, R. & Moran, J. (1988). Increased attention enhances both behavioral and neuronal performance. *Science*, 240, 338-340.
 Sullivan, G. D., Oatley, K. & Sutherland, N. S. (1972). Vernier acuity as affected by target length and separation. *Perception & Psychophysics*, 12, 438-444.
 Watt, R. J., Morgan, M. J. & Ward, R. M. (1983). The use of different cues in vernier acuity. *Vision Research*, 23, 991-995.
 Waugh, S. J., Levi, D. M. & Carney, T. (1993). Orientation, masking, and vernier acuity for line targets. *Vision Research*, 33, 1619-1638.

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- Wilson, H. R. (1986). Responses of spatial mechanisms can explain hyperacuity. *Vision Research*, 26, 453–469.
- Wilson, H. R., McFarlane, D. K. & Phillips, G. C. (1983). Spatial frequency tuning of orientation selective units estimated by oblique masking. *Vision Research*, 23, 873–882.
- Vogels, R. & Orban, G. A. (1985). The effect of practice on the oblique effect in line orientation judgments. *Vision Research*, 25, 1679–1687.
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